THE LARVA OF *HEMIPHLEBIA MIRABILIS* SELYS (ODONATA).

By R. J. Tillyard, M.A., Sc.D. (Cantab.), D.Sc. (Sydney), F.R.S., F.N.Z.Inst., F.L.S., F.G.S., F.E.S., C.M.Z.S.

(Thirteen Text-figures.)

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Hemiphlebia mirabilis Selys is a tiny metallic green damselfly of very great morphological and phylogenetic interest. It is entirely confined to Australia, the only known localities for it so far being Port Denison (Bowen) in Queensland (the type locality), and Alexandra, Victoria. It is one of the smallest of living dragonflies, its expanse of wing being only three-quarters of an inch or a little more. De Selys (1877) placed it at the very end of his group or "legion" *Agrion* of the subfamily Agrioninae, next to the genus *Agriocnemis*; in more modern classification, this would put it at the end of the family Coenagriidae. In 1913 (p. 463) I described the appendages of the male and recorded the peculiar mode of courtship of these tiny insects amongst the reed-masses of the backwaters of the Goulburn River at Alexandra, where I studied the insect in December, 1906. Later, I sent specimens to Professor C. H. Kennedy at Columbus, Ohio, for the study of the penis of the male. He came to the startling conclusion that this little insect had one of the most generalized forms of penis known within the Order Odonata (Kennedy, 1920). Later still, the discovery of ancient forms of Zygopterous dragonflies in the Lower and Upper Permian (Tillyard, 1925, 1926*a*, 1928) indicated a very close relationship between the original ancestral type of the whole Order Odonata and this Australian genus, while a detailed comparison of the wing-venations made it quite clear that *Hemiphlebia* stood quite isolated amongst existing forms and must be regarded as the sole representative of a distinct family Hemiphlebiidae (Kennedy, 1920; Tillyard, 1926*b*) standing at the very base of the Zygoptera.

It will thus be seen that the progress of researches on the Order Odonata, in the course of the last twenty years, has picked out this obscure Australian genus from a mass of unrelated forms and set it up as one of the key-genera for the right understanding of Odonate phy'ogeny. As soon as this had been done, it at once became of the utmost interest that the larva should be discovered and studied also, in order that we might see what evidence was available from such important larval characters as the wing-tracheation, the labial mask, the mandibles, the gizzard and the caudal gills. The opportunity to do this presented itself when the Commonwealth Government recently invited me to visit Australia in connection with the organization of entomological research. Arrangements were made to spend a long week-end at Alexandra some time in November. Through the kindness of Mr. Michael Martin, Manager of Sulphates Proprietary Ltd., of 395, Collins Street, Melbourne, and Mr. C. R. Lyne, of Hartley's Proprietary, Ltd., 270, Flinders Street, Melbourne, a private car was placed at my disposal, and a party was

formed of these two gentlemen, both of whom are keenly interested in trout-fishing, Mr. G. F. Hill, F.E.S., Entomologist to the Commonwealth Council for Scientific and Industrial Research, Mr. J. Clark, Entomologist to the National Museum, Melbourne, and myself. We drove out to Alexandra, a distance of close on one hundred miles from Melbourne, on Saturday, 5th November last, and worked the Goulburn River the same evening and on the Sunday and Monday following. I wish here to express to all these gentlemen my very sincere thanks for the assistance given me in this undertaking. I also wish to thank Mr. A. L. Tonnoir for assistance in the preparation of slides and for the drawing of Text-fig. 8; and Mr. W. C. Davies for enlarging the photograph reproduced in Text-fig. A.

Text-fig. A.—Backwater of the Goulburn River, near Alexandra, Vic., showing reed-beds in foreground, where larvae of *Hemiphlebia mirabilis* Sel. were found. Mr. J. Clark, F.E.S., with dredging-net.

[Photo. by R. J. Tillyard.

My previous visit to Alexandra was in December, 1906, or nearly twenty-one years earlier. Owing to the long period of time that had elapsed, my memory of the intricate backwaters of the Goulburn River was not sufficiently clear for us to locate, at the first attempt, the exact place where the tiny insect had been found before. As the dragonflies themselves had been taken on the wing on 22nd and 23rd December, we did not expect to find any of them about early in November, but we hoped to discover the full-fed larvae. About two hours were spent on the Saturday evening searching for the original locality, but without success. On the Sunday morning the search was continued, and I extended my survey of the backwaters to a distance of well over a mile above the bridge before I suddenly came upon the very clumps of reeds where I had first seen the tiny insects executing their delightful mating dances. We discovered later that

there was a good reason why the insect was confined to this small area; for, during the periodical droughts that occur, all the rest of the huge backwaters dry up; but, just at this point (Text-fig. A) there is a rather deep hole between the clumps of reeds, and this serves as a reservoir for the larvae when no other water is available.

The position having been located, all five of us got to work with nets, scoops and sharp knives. The reeds were cut off in clumps, close to their roots; the water-weeds were dredged up in masses; the bottom mud was scooped up and examined; in fact, everything was done to ensure that the larvae should not escape us. Preliminary exploration of the rest of the backwater had yielded only a few common types of damselfly larvae, viz. *Austrolestes analis* Ramb., *A. leda* Sel., *Ischnura heterosticta* Burm. and *Austroagrion cyane* Sel. I was looking for a damselfly larva of a type unknown to me, since that would almost certainly prove to be *Hemiphlebia*. We worked for well over an hour before I noticed a small, dark brown, sluggish larva separate itself from a tangled mass of reed-stems and water-weed. An examination of this larva showed that it was of a type new to me, so we decided to continue searching for more, and to take them back alive to the hotel at Alexandra, where I had the necessary microscopes and dissecting instruments ready. At the end of three hours' work we had about two dozen, most of which had been found clinging closely to the lower portions of the stems of the weed *Myriophyllum*, while a few were found clinging to the bases of the stems of reeds and submerged grasses. The lower leaves of *Myriophyllum* are of a dirty brownish colour, and the larvae were practically invisible in such a position until they moved.

During the same afternoon, I dissected and studied four of these larvae and was soon able to determine them definitely as larvae of *Hemiphlebia*. The first diagnostic character used was the absence of the basal cross-vein closing the quadrilateral in the forewing; this was very clearly shown in all well-grown larvae. The only other dragonfly at present existing which possesses this character is *Chorismagrion risi* Morton from North Queensland; this is about four times as large as *Hemiphlebia mirabilis*. Apart from this, it soon became evident that the larvae possessed a number of other unique and unexpected characters which rendered it even more important from the viewpoint of phylogeny than I had imagined it would be.

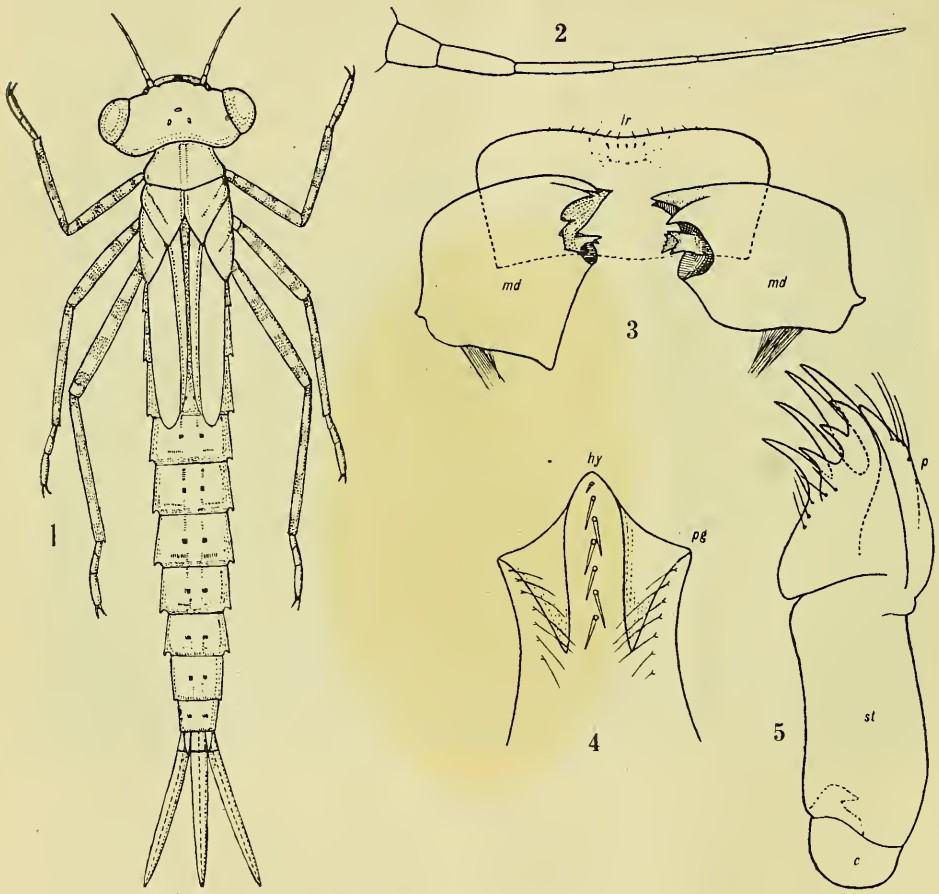
Accompanied by Messrs. Lyne and Clark, I again visited the locality on the Monday morning, our captures for about two hours' work amounting to twenty-six, all found within a few yards of the original reed-clumps where I had first taken the dragonfly. Thus we returned from Alexandra with fifty of these larvae, some alive and some carefully preserved in Blé's solution. All of these were in the last instar, and some must have been within a week of emergence, judging by the clear formation of the imaginal antennae and tarsal claws inside the larval organs.

Description of the Larva. Text-figs. 1-12.

Total length including caudal gills (average), 13·5 mm.; length of abdomen, 7·5 mm.; breadth across head, 2·5 mm., across sixth abdominal segment, 1·5 mm.; length of wing sheath, 3·1 mm., of antenna, 1·4 mm., of caudal gills (lateral), 2·5 mm.; of paraprocts (cercoids), 0·5 mm.; lengths of femur, tibia and tarsus respectively: fore leg, 1·5, 1·6, 1·0 mm.; middle leg, 1·8, 2·0, 1·2 mm.; hind leg, 2·5, 2·5, 1·3 mm., the tarsal measurements including the claws.

General colouration a dull, medium or dark brownish, with very little pattern except on the legs, which are banded with darker brown as shown in Text-fig. 1.

Head more than twice as wide as long, only slightly concave posteriorly between the moderately prominent postocular lobes, which are rounded. Compound eyes prominent, dark brown, button-like; ocelli distinct, dark brown; antennae



Text-figs. 1-5.—*Hemiphlebia mirabilis* Sel.
1. Full-grown larva. Length, including gills, 13·5 mm. 2. Antenna of full-grown larva. Length 1·4 mm. 3. Labrum (*lr*) and mandibles (*md*) of full-grown larva (× 50). 4. Hypopharynx (*hy*) and paragnaths (*pg*) of full-grown larva (× 75). 5. First maxilla of full-grown larva (× 75). *c*, cardo; *p*, palpus; *st*, stipes.

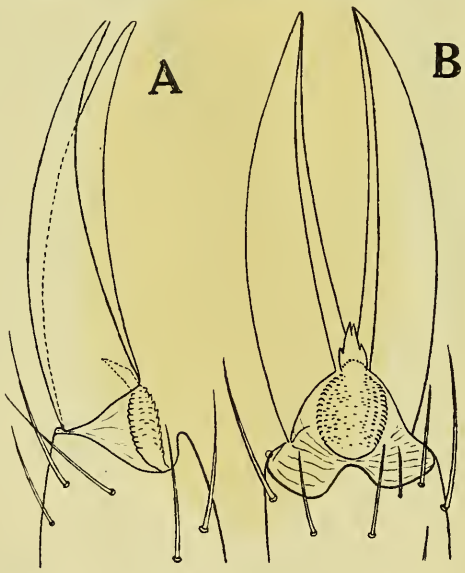
smooth, hairless, rather long, 1·4 mm., consisting of seven segments, of which the first or scape is somewhat swollen, subconical, half as long again as wide, the second or pedicel longer and less swollen, about three times as long as wide, and the other five, or distalia, are elongated and very slender (Text-fig. 2); ratios of the lengths of the segments from base to apex, 14 : 20 : 26 : 22 : 20 : 18 : 17. Labrum (Text-fig. 3) more than twice as wide as deep; margin well rounded

laterally, slightly emarginate medially, with a few short, weak setae on the median portion and a few small, scattered sensillae just above them around the median line on the epipharynx. Mandibles (Text-fig. 3) very stout and strong, markedly asymmetrical, of primitive type, showing clearly differentiated incisor and molar areas on the inner or cutting surface; the right mandible has three strong teeth placed close together near the apex of the incisor area, with a smaller one on the inner margin well removed towards the molar portion; the latter carries a strongly projecting bifid prong; the left mandible has three strong incisor teeth, two at the apex and one somewhat removed and turned curvingly inwards, while the molar area carries a much larger projection than that of the corresponding area of the right mandible; this projection has a broad, hollowed out apex, split open on the inner side, and bordered elsewhere by six irregular teeth, four fairly large and two very small. It would appear that the prong of the right mandible works into the hollow of the larger process on

Text-figs. 6, 7.—*Hemiphlebia mirabilis* Sel.
6. Labial mask of full-grown larva (× 45). *ll*. lateral lobe; *mh*, movable hook; *ml*, median lobe; *mt*, mentum. 7. Lateral lobe of same (× 140). *mh*. movable hook; *s*, seta of same.

the left mandible, while the incisor teeth of one side fit more or less accurately into the clefts between those of the other. Hypopharynx (Text-fig. 4) remarkably well developed, with prominent median tongue and strongly projecting side-lobes or paragnaths; the former carries a median row of strong setae directed inwards, while the latter each bear a row of about seven long, slender hairs. Maxillae (Text-fig. 5) with short cardo, elongate stipes, and well developed inner lobe carrying two sets of teeth, the outer four in number, long and rather slender, the inner three in number, shorter and broader; the former may represent the marginal armature of the galea, the latter that of the lacinia; a few stiff hairs situated just basally from the teeth; palp short, its tooth-like apex projecting not quite as far distad as the first lacinial tooth, its outer margin at about one-third from apex slightly humped and carrying four slender, long hairs. Labial

mask (Text-figs. 6, 7) very long and slender, 3 mm. when fully extended, with long, narrow submentum, strong hinge, mentum narrow basally but expanding widely distally; median lobe with slight indication of separation from mentum proper, and consisting of a pair of broad, flat lobes with crenulate outer margins, separated by a very deep, narrow cleft, and a pair of well separated, prong-like processes of large size, nearly as large as the movable hooks of the lateral lobes, but curved in the opposite direction; there is a stiff seta close to the base of each prong, on the side removed from the middle line. Lateral lobes of complex structure; movable hook large and strong, with a single seta projecting inwards at right angles and situated very close to the base of the hook; no other setae present on lateral lobes at all; distal margin carrying a strong tooth similar to, and nearly as large as the movable hook, and a much shorter, irregularly denticulate process; apex of lateral lobe projecting as a strong, slightly nodding tooth, with its free inner margin convexly curved and very slightly crenulate. Text-fig. 7 shows all these structures enlarged.



Text-fig. 8.—*Hemiphlebia mirabilis* Sel. Tarsal claws of full-grown larva (× 220). A, lateral, B, ventral view. (*Drawn by A. L. Tonnoir.*)

Thorax: Prothorax about half as wide as head posteriorly, but considerably narrowed anteriorly; smooth, without tubercles. Pterothorax (= meso- plus metathorax) also smooth, without hairs or tubercles of any kind; spiracles of mesothorax clearly marked, those of metathorax indistinct; wing-sheaths projecting backwards subparallel to one another for a distance of about 3 mm., the apices of the hind wing-sheaths just overlapping the distal margin of the third abdominal segment. Wing-venation very strongly indicated, pale creamy on a dark brown wing-sheath. Wing-tracheation described separately below (p. 201).

Legs rather long, pale semi-transparent brownish with darker banding on the femora and tibiae, as shown in Text-fig. 1; tarsal claws without an internal tooth, but with a small, curiously formed, retractile pad or arolium projecting

between their bases (Text-fig. 8); this pad is in the form of a broadly oval area of rugose chitin situated in the middle of the soft membrane at the bases of the claws, and having a peculiar toothed projection distally; when the claws are retracted, the whole of the pad folds in between the claws and the tarsus, and is protected externally by a marked mid-ventral process from the end of the last segment of the latter.

Abdomen subcylindrical, somewhat flattened ventrally, the first six segments very nearly of equal width, the rest tapering towards the anal end, the tenth segment being little more than half the width of the seventh; first segment short, second to eighth segments each about two-thirds as long as wide; first eight segments slightly narrower basally than distally, the distal border ending posteriorly on each side in a small, backwardly projecting spine. Colour-pattern indistinct, the chief markings being a pair of dark brown spots not very close together near the mid-dorsal surface of each segment; segment 10 also has two less distinct spots placed dorsolaterally; there is also a slight indication of a somewhat paler mid-longitudinal line and a darkening of the posterior margin of each segment. Paraprocts (cercoids) clearly visible, 0·5 mm. long, pointed. Caudal gills (Text-fig. 9) held in the living insect not very wide apart, the median gill only slightly raised, the laterals slightly lowered and only moderately diverging; lateral gills 2·0 to 2·6 mm., the median very slightly shorter and broader. Each lateral gill is a rather broad vertical lamella, suboval in shape, broadest at about two-thirds from base, and almost completely rounded at its apex, except for a very small and obtuse apical angle; the upper edge of the lamella is fringed with abundant soft hairs, very short along the basal half, but becoming longer and more conspicuous distally up to within a very short distance of the apex, and interspersed here and there with short spines; the lower edge is armed with a series of closely set, short spines or setae directed forward and outward, and mostly separated by delicate but slightly longer hairs; the midrib is slightly curved towards the lower edge and considerably nearer to it than to the upper; it is armed on the outer side only by a series of about twenty to twenty-five short but stout spines, with rudiments of one or two more close to the base. The median gill (Text-fig. 9) is slightly broader and more symmetrical in shape, with its midrib straighter, and armed, near the base, on both sides, with eight to ten short, stout spines of the type seen in the lateral gills; the upper edge is armed similarly to the lower edge of the lateral gill, and *vice versa*. The tracheal supply closely resembles that of the gills of the genus *Synlestes* (Tillyard, 1917, p. 193, fig. 84A), the main tracheal trunks being stout and following the midrib, while the branch tracheae come off obliquely and branch very little. The colour of the gills is semi-transparent brown, sometimes with considerable development of deep rose-pink or purple bordering the midrib, and slighter indication of darker patches of pigment irregularly placed elsewhere. The breaking joint of each gill is very strongly marked, situated nearly 0·5 mm. from the gill-base (Text-fig. 9, *bj*); the two main longitudinal tracheae are quite large where they pass the joint, but the gills become detached very easily and apparently without any damage to the larva, as one finds quite a number of them without their gills.

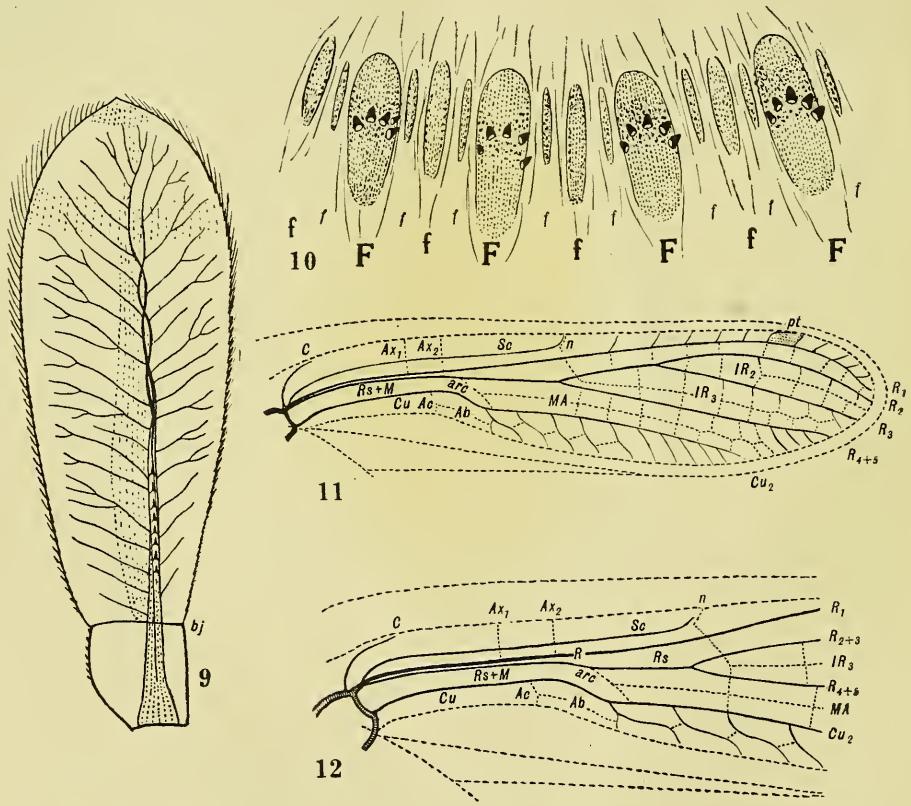
Rectal breathing takes place, but apparently very sluggishly. When opened, the rectum is seen to contain three large longitudinal folds, one dorsal and two latero-ventral, separated by three very small folds, two latero-dorsal and one ventral. These folds receive a special tracheal supply but only a poorly developed

one; they are evidently rudimentary rectal gills of the type found in other Zygopterous larvae (see Calvert, 1915, pp. 387-8).

Gizzard (Text-fig. 10) unique in consisting of three very distinct types of chitinous folds, as follows:—

(*a*) Major folds, denoted by **F**, which are broad, oval cushions, four in number, each covered with fine denticulations and also carrying five very large teeth, arranged in a transverse arch, as in the family Lestidae. The average length of each major fold is 0·37 mm., greatest breadth 0·12 mm.

(*b*) Medium folds, denoted by **f**, which are much narrower cushions, four in number, covered with fine denticulations only. Average length, 0·25 mm., greatest breadth 0·05 mm.



Text-figs. 9-12.—*Hemiphlebia mirabilis* Sel.

9. Median caudal gill of full-grown larva, showing breaking-joint (*bj*). Length 2·5 mm. 10. Gizzard of full-grown larva (× 56), opened by a longitudinal cut. **F**, major fold; **f**, medium fold; *f*, minor fold. 11. Last larval instar, sheath of forewing (× 27). 12. Basal portion of forewing sheath from another specimen, more greatly enlarged (× 36). *Ab*, anal bridge; *Ac*, anal crossing; *arc*, arculus; Ax_1, Ax_2, the two antenodals; *C*, costal trachea; *Cu*, cubital trachea; IR_2, IR_3, convex veins interpolated between concave branches of radial sector; *MA*, anterior median vein; *n*, nodus; *pt*, pterostigma; *R*, radial trachea; R_1, its main branch; *Rs*, radial sector trachea, with its branch tracheae R_2, R_3 and R_{4+5}; *Rs* + *M*, trachea supplying *Rs* (and *MA* in other Odonata); *Sc*, subcostal trachea.

(*c*) Minor folds, denoted by *f*, which are even shorter and very much narrower chitinous areas, eight in number, covered with fine denticulations only. Average length 0·18 mm., greatest breadth 0·02 mm.

The four major folds alternate with the four medium folds, and these eight are again separated by the eight minor folds which alternate with them. The gizzard is thus seen to consist of sixteen folds, only four of which carry large teeth. Using Higgins' Notation, the formula for the gizzard is 4 (F, 5 — *f*, 0 — f, 0 — *f*, 0).

This is the only known Odonate gizzard having three types of chitinous folds, and appears to be a survival of the primitive type from which all the others can be derived. The eight-fold Lestid gizzard has clearly evolved from it by suppression of the eight minor folds, the medium folds of *Hemiphlebia* becoming the so-called "minor folds" of Lestidae. The more normal sixteen-fold Zygopterous gizzard has arisen by the equalling-up of the four medium and four major folds, while the minor folds of *Hemiphlebia* have remained the minor folds of other Zygoptera. The eight-fold gizzard of Petaluridae must have arisen by suppression of the eight minor folds and equalling-up of the remainder, while the four-fold gizzards of other Anisoptera have evolved by suppression of all except the four major folds in *Hemiphlebia*.

Habitat.—Backwaters of the Goulburn River, Alexandra, Victoria; 6th and 7th November, 1927.

Description of the Larval Wing-tracheation. Text-figs. 11, 12.

Altogether, six larvae were dissected and studied for their wing-tracheation, viz. four at Alexandra on 6th November, and two more from those brought back alive to Melbourne, on 8th November, 1927. All six gave almost exactly the same results, the only differences being individual ones of quite minor value, such as slight variation in the number and position of certain cross-veins. The results obtained are so striking that I should have little hesitation in claiming family rank for the genus *Hemiphlebia* on them alone.

Taking first of all the basal tracheal trunk, we notice two peculiarities not found in other Odonate larval wings, viz. that tracheae Sc, R and Rs + M (this latter being the trachea called M by Needham) all come off by a short, stout, common stalk, and that there is absolutely no sign of an anal trachea, Cu coming off by itself at a point well removed from the subcosto-radial group. In all other Odonate larval wings so far studied, Sc, R and Rs + M come off separately from the basal trunk, though R and Rs + M are always very close together; also trachea A arises somewhat posteriad from Cu, approaches it closely for a short distance, and then either ends or diverges from Cu again by way of the anal crossing, Ac.

But the most striking feature about the tracheation is the complete absence of any tracheae along the courses of the convex veins, IR_2, IR_3 and MA, which are just those veins which I have claimed, on palaeontological grounds alone, to have been interpolated or added to an originally simpler venational type, such as can be found in the Palaeodictyoptera and Megasecoptera. In all other Odonate larvae, tracheae are present for IR_3 and MA, but not for IR_2 (M_{1A} of Needham). The tracheal supply of IR_3 (Rs of Needham) varies in different groups. Most of the Zygoptera have the trachea corresponding entirely with the vein IR_3. But the Lestidae have the tracheal supply of vein IR_3 developed from the anterior vein R_3, close to its origin, via the oblique vein, leaving the basal portion of

vein IR_3 without tracheal supply (the "long bridge"). In the Anisoptera, an even more complex method of supply is developed by means of a trachea descending from R at the subnodus, crossing R_2 and R_3, entering IR_3 by the oblique vein, and leaving the short basal portion, or "bridge", unsupplied by any trachea.

One consequence of the absence of the tracheae mentioned above is that there does not appear to be, in the larva of *Hemiphlebia*, any trachea which can rightly be designated as belonging to the media; for the posterior media, MP, is absent, and the anterior MA, has no tracheal supply. While, therefore, retaining the notation Rs + M for the basal trachea below R, since it supplies both Rs and MA in all Odonate larvae other than *Hemiphlebia*, it is necessary to point out that the available evidence is quite compatible with the hypothesis that this trachea may be merely Rs, and that trachea M may have disappeared with vein MP before the interpolated vein MA received any tracheal supply. This would account for the condition found in *Hemiphlebia* larvae better than any other hypothesis.

Another interesting condition of the tracheation is the series of descending branchlets of trachea Cu_2. The first of these arises just before the distal angle of the quadrilateral, and divides into a short basal and longer distal branch; from the short basal branch, a pigment band (the anal bridge, Ab) runs back to the anal crossing, Ac, which is also without any trachea. The second, third, fourth and fifth branchlets are simple, but somewhat curved; these and the distal branch of the first are connected by oblique pigment-bands representing specialized cross-veins in the imaginal wing, which help to make up the distal portion of the composite vein 1A. The more distal branchlets are shorter and straighter descending tracheae corresponding exactly with the distal branch veinlets in the imaginal wing. A series of similar short branchlets, four in number, is to be found descending from the distal end of R_{4+5}. There are no tracheae preceding the two antenodals, but all the postnodals (five in number), the two veins forming the basal and distal sides of the pterostigma, and the veins in the space beyond the pterostigma, are preceded in the larval wing by delicate tracheae. R_3 has a single, short, branch trachea near its apex, R_2 none. Sc is simple, the end of its trachea turning upwards to the costa at the nodus; the subnodus has no trachea at all, but its pigment band descends exactly on to the origin of IR_3 (Rs of Needham).

The open discoidal cell or quadrilateral of the forewing of *Hemiphlebia* is well shown in the larval wing, and is there seen to be of exceedingly simple formation. The trachea Rs + M diverges but slightly from trachea R_1, while trachea Cu_2 runs subparallel to it below, and very slightly approaching it up to the level of the second antenodal, Ax_2. About this point, Cu_2 takes a marked curve of flattened sigmoid form, thus nearly doubling its perpendicular distance from Rs + M by the time its first descending branchlet is given off. The two main tracheae, Rs + M above and Cu_2 below, are here connected by a strong pigment band representing an obliquely placed crossvein, which forms the distal side of the quadrilateral in the imaginal wing, and from the middle of which the pigment band of vein MA arises. The very obvious resemblance between this formation and those at the proximal ends of the other interpolated veins, IR_2 and IR_3, and also the formation at the meeting of Ac and Ab, must not be lost sight of.

The entire absence of trachea 1A might seem puzzling at first to those chiefly acquainted with the tracheation of Anisopterous larval wings. In Zygopterous larvae, however, this trachea is always exceedingly weak, and quite frequently

does not reach as far as Ac, as is well shown by Dr. Ris' excellent photographs of *Agrion* (*Calopteryx*) *splendens* (Tillyard, 1915, Pl. xxxiv) and by my own photographs and drawings of *Diphlebia lestoides* (1915, p. 217, Text-fig. 3, and Pl. xxxii).

General Discussion of Larval Characters.

It will be clear, I think, from the above description of the larval characters that we have to deal with a very archaic type. This conclusion is not based upon the form of any single organ, and might quite well be arrived at independently of the wing-tracheation. In order to exhibit the generalized relationships indicated by a study of the larval characters, these latter are now considered in groups according as they are unique for the Order, or show affinities with those of other families or groups of Odonata:—

(1) *Characters unique within the Order Odonata..*

(*a*). *The trifid hypopharynx.*—The most primitive groups of Insects have this character well marked, the hypopharynx consisting of a median tongue with two supporting lateral paragnaths, sometimes called "maxillulae". This type is well seen in Machilidae and also throughout the Order Plectoptera. The trifid form seen in *Hemiphlebia* larva is not unlike the stage found in the imago of most Neuroptera.

(*b*). *The presence of both glossae and paraglossae in the labial mask.*—No mask with both processes fully developed has hitherto been found in the Odonata, but a pair of minute teeth on the median lobe in a few archaic genera (e.g. *Cora*, Calvert, 1911, p. 53, fig. 28) has been interpreted as probably indicating the vestiges of the glossae. The presence of the large prongs in *Hemiphlebia* larva shows that this interpretation may possibly be correct; at the same time, the condition in *Hemiphlebia* must be regarded as very much more primitive than anything else at present known within the Order.

In view of the form of the median lobe in larvae of Plectoptera, it might be preferable to maintain that the broad lobes separated by the narrow cleft were actually the glossae, while the prongs were the paraglossae. This interpretation has the advantage of deriving the median cleft (admittedly an archaic character in Odonata) without change from an ancestor shared in common with Mayflies and other archaic insects, all of which possess such a cleft. If it be accepted, then the vestigial teeth mentioned above must be regarded as remnants of the paraglossae.

But, whichever interpretation we may adopt, it is clear that the median lobe of the labial mask in *Hemiphlebia* is unique in possessing both pairs of gnathobases well developed, as in the most primitive insects.

(*c*). *The incomplete wing-tracheation.*—The absence of tracheae for veins IR_3 and MA is unique within the Order. Vein IR_2 is never preceded by a trachea in any Odonate; hence it has never been considered a true branch of a main vein, though the fossil record shows that it has just as much claim to that status as IR_3 or MA. Most Odonata have a delicate anal trachea; but, as already pointed out, it is very feebly developed in many Zygoptera and its capture of the descending veinlet Ac appears to have been a secondary development.

(*d*). *The origin of tracheae* Sc, R_1 *and* Rs + M *from a short common stalk.*—The nearest parallel to this is to be found within the Order Plectoptera, where the subcosto-radial group of tracheae usually arises from a single long stalk, though sometimes from two tracheae arising very close together; (M sometimes arises from this same stalk, sometimes separately from the basal trunk).

The general indication given by the above unique archaic characters is for a somewhat distant relationship with the Plectoptera.

(2) *Characters shared with the Synlestidae.*

(*a*). *The form of the caudal gills.*—These are so close to those of the genus *Synlestes*, particularly to *S. albicauda* Till., that on this character alone one would classify *Hemiphlebia* as a member of the family Synlestidae. The shortness of the gills, their general shape, the oblique position of the branch tracheae, the armature, pigmentation and semi-opacity, all closely agree with the Synlestid type of gill. In addition, the gills are held by the living larva in the same manner as in the case of *Synlestes*, viz. with the three gills very slightly apart, the median one only slightly raised and the laterals only slightly depressed and diverging.

(*b*). *The gizzard.*—This resembles that of the Synlestidae and Lestidae in the arrangement of the teeth and their confinement to four major folds. These two families, however, possess gizzards with only eight folds (four major and four minor), whereas all other Zygoptera have 16-fold gizzards, while all the Anisoptera except the Petaluridae have 4-fold gizzards. The resemblance is closer to the Lestidae than to the Synlestidae.

(*c*). *The labial mask.*—The Synlestid characters of the mask are to be found in the prominent median lobe, with deep median cleft, and in the form of the apical tooth of the lateral lobe, and the finely crenulate inner border of the same.

(*d*). *The larval habits and colouration.*—These closely resemble those of the genus *Synlestes*, and the general facies of the larva can be said to be more Synlestid than anything else, though lacking the elongation of the body and antennae so noticeable in the genus *Synlestes* itself.

The above larval characters indicate a close affinity with the Synlestidae, but are greatly strengthened by a number of imaginal characters, such as the general facies, the metallic green colouring, numerous points of resemblance in the wing-venation, and particularly by the fact that *Chorismagrion*, a very close ally of *Synlestes*, is the only other known genus in which the quadrilateral is ever open basally.

(3) *Characters shared with the Lestidae.*

(*a*). *The gizzard.*—The resemblance of this to the Lestid gizzard has already been mentioned above. The presence of five large teeth on each of four major folds, the teeth being arranged in a transverse arch, is a striking Lestid character.

(*b*). *The presence of setae on the movable hook of the mask.*—This character has hitherto been found only in the Lestidae, which have either two or three strong setae on the movable hook. *Hemiphlebia*, with a single strong seta close to the base of the hook, here shows unmistakable affinities to the Lestidae.

(*c*). *The dentition of the lateral lobe of the mask.*—The division of the lobe into two large teeth and an irregularly denticulated process is closely paralleled by such species as *Austrolestes analis* Ramb. (Tillyard, 1917, p. 83, fig. 32, H), but the process is more evenly truncated and regularly crenulated in the latter, while the whole lobe is more broadened out and tends towards the spoon-shaped type. There is, however, no other type of lateral lobe which shows so close a resemblance to that of *Hemiphlebia*.

(4) *Characters shared with the Libellaginidae and Agriidae (Calopteryginae of de Selys).*

(*a*). *General form of the labial mask.*—In both groups this is very long and slender, and generally of similar shape. The median lobe in Libellaginidae (*Micromerus* and *Rhinocypha*, see Fraser, 1922, pp. 79-81, Pl. ix, x) is of the same form as that of *Hemiphlebia*, the median cleft perhaps not quite so deep, but slightly wider, and there is the same indication of a slight constriction or division between the median lobe and the mentum proper; the large prongs and the setae, however, are entirely absent. The very prominent and deeply cleft median lobe of Agriidae may be regarded as a specialization from the Libellaginid type.

As regards the lateral lobes, setae are developed at the base of these in both Libellaginidae and Agriidae, but never on the movable hooks. The form of the lateral lobe is elongated and slender, with large movable hook and two sharp teeth, with or without a smaller tooth between them. This type cannot be regarded as coming very close to that of *Hemiphlebia*.

(*b*). *General habits of the larvae.*—The habits of the larvae of *Hemiphlebia* and Agriidae appear to be closely alike. Both are sluggish creatures which cling to the bases of reed-stems, weeds, etc., in still or slowly moving waters, and have a dull colouration.

(5) *Characters shared with the Epallagidae and Polythoridae.*

(*a*). *Mandibles with distinct molar and incisor areas.*—These so-called "biramous" mandibles are admittedly archaic, and are characteristic of the Machilidae and the whole Order Plectoptera. They have been recorded for the Epallagid genus *Pseudophaea* and the Polythorid genus *Cora* (see Calvert, 1911, p. 56). The differentiation of the two areas is, however, more clearly marked in *Hemiphlebia*, in which the form of the mandibles approaches more closely to those of the Plectoptera than in any other known Odonate.

(6) *Characters shared with the Coenagriidae (Agrioninae of de Selys).*

As *Hemiphlebia* has always been classified with this family until I removed it in 1926, one naturally expects to find some close resemblances in the larval characters. But, curiously enough, none is to be found, unless one allows the purely negative character of the absence of any specialized tracheal formation in the larval wings giving origin to an oblique-vein formation in the imago, and, also, the resemblance of the truncated process of the lateral lobe of the labial mask to a somewhat similar process in most Coenagriidae, though the latter have no large tooth between the process and the movable hook. The general forms of the two types of mask are very distinct, and the same is true of the gills, gizzard and other larval structures. One can only conclude that the genus *Hemiphlebia* was wrongly placed by de Selys, and that no close relationships exist between it and the Coenagriidae.

The general conclusions which we may make from the above facts are that the larva of *Hemiphlebia* is an exceedingly archaic type, probably by far the most archaic larval type of Odonata still existing; it shows a closer relationship with the larval forms of the Order Plectoptera than might reasonably be expected, though that relationship is still a distant one, indicating a common ancestor very far back; it shows, more particularly, a very close relationship with the Synlestidae and Lestidae, and is properly to be placed close to these two families in any scheme of classification. The erection of the family Hemiphlebiidae appears to be

more than justified on the larval characters alone, and the family may legitimately be regarded as a remnant of an exceedingly early type of Zygoptera, closely related to the known Permian forms, and thus not really very far removed from the original types (now lost) which gave origin to all the greater groups of Odonata, viz. the Coenagrioidea, Agrioidea, Anisozygoptera, and, through them, the Anisoptera.

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